Male Mate-Locating Behavior in the Desert Hackberry Butterfly, *Asterocampa leilia* (Nymphalidae)

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Abstract. The mating system of the desert hackberry butterfly, *Astero-campa leilia*, is described with special reference to the site tenacious mate-locating behavior of the males. Males occupy perches on or next to the larval foodplant, desert hackberry (*Celtis pallida*). Other males are not tolerated within several meters of a male's perch site and are chased away when they fly nearby. Males occupy perch sites in the morning. Some hackberry trees are more likely to be used as perch sites than others and males at these sites experience the highest rate of contacts with females and other males. Females passing a perch site are chased, courted, and, if receptive, mated. The data indicate that males defend perch sites as a means of maximizing potential contacts with newly-emerged, virgin females leaving the plant adjacent to their perch site.

Introduction

Male butterflies show a wide interspecific diversity in the extent to which they are site tenacious in their mate-locating behavior (Scott, 1974, 1975, 1982). At one extreme males are not tied to any given site but fly widely through the environment searching for females. This strategy has classically been referred to as patrolling. At the other extreme males are very site tenacious and an individual may defend a space on a hilltop or other place for several days usually during some restricted daily activity period (Powell, 1968; Baker, 1972; Douwes, 1975; Suzuki, 1976; Davies, 1978; Bitzer & Shaw, 1979, 1983; Callaghan, 1982; Lederhouse, 1982; Alcock, 1983, 1985; Wickman & Wiklund, 1983; Knapton, 1985; Wickman, 1985; Alcock & O'Neill, 1986). In territorial species males interact with other males in ways that are very different from their interactions with females. Aerial combat occurs in the form of ascending flights and wing contact. Between these extremes of patrolling and highly territorial species there are species in which males, although showing some site tenacity,

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may only briefly occupy a site and be less aggressive toward conspecifics. Detailed studies of these behaviors are lacking.

Males of the desert hackberry butterfly (*Asterocampa leilia* Edwards) occupy perch sites near the larval foodplant, desert hackberry (*Celtis pallida* Torrey), that they appear to defend against conspecific males (Austin, 1977). Our preliminary observations of this species in central Arizona suggested that individual males do not spend much time on specific sites. Here we describe in detail the perching behavior of the males of this species and document the extent to which males are site tenacious and their perch site preferences. The discussion focuses on the ecological circumstances favoring this sort of mate-locating behavior, especially in comparison with mate-locating techniques in other species.

METHODS

Asterocampa leilia males and females were observed and collected at two flat or gently sloping sites near water courses in the upper Sonoran desert habitat typical of central Arizona. Our primary site was near the Salt River about 40 km northeast of Tempe, Arizona, and the other site, used primarily for observations of courtship with hand-reared females, was along Sycamore Creek about 70 km from Tempe. At both sites the large vegetation included paloverde (*Cercidium* spp.), mesquite (*Prosopis* spp.), saguaro cactus (*Carnegia giganteus* (Engelmann) Britton and Rose) and desert hackberry (*Celtis pallida*).

At the Salt River site we identified a triangular, 1700 m^2 area that extended on the north to the beginning of a small mountain range, on the south to a line of paloverde trees, on the west to a low ridge extending out from the mountains, and on the east to a small dry wash. This area contained fifteen discrete clumps of hackberry that varied in size. Males were captured and carefully marked by writing numbers on the dorsal and ventral hindwings with a felt-tipped marking pen (Sanford Sharpie[R]).

On 17 mornings from 6 May to 11 June in 1985 we walked through the study area at 30 min intervals and noted the location and identity, if marked, of each male seen perched. We also observed the activities of males at individual perch sites, especially those that were most often occupied, and recorded the interactions between the perch site occupant and intruding individuals of both sexes. Wherever possible these observations were made on marked males that occupied perch sites.

Courtship, Copulation, and Spermatophore Counts

Successful courtships and the ensuing copulations were elicited by releasing hand-reared virgin females near perched males in the field. The females were reared from eggs collected by placing field-caught females in cages with a sprig of the larval foodplant.

After copulation, mated pairs were killed and stored by freezing. Later the females were thawed, weighed, and dissected under insect Ringer's solution. The bursa copulatrix of each female with its contents was examined and weighed to the nearest 0.01 mg. The male of each pair was also thawed and weighed.

To estimate the frequency with which females mate, we collected and froze a sample of females from the population. They were later thawed and dissected under insect Ringer's solution, and the contents of the bursa copulatrix of each was examined. The wing wear of these females was assessed as an indicator of age. Each female was placed in one of three wing wear categories: fresh — little or no scale loss or tattering, worn — substantial scale loss or tattering on one or two wings, and very worn — substantial scale loss or tattering on all wings.

Statistical Summary and Tests

Parametric summary statistics are given as the mean ± the standard deviation. The results of all statistical tests were evaluated at the 0.05 level of significance.

RESULTS

Spatial Organization and Daily Pattern of Male Activity

Male perch sites were found in only 20 locations within the Salt River study area. A perch site was an area of approximately 1-2 m² in all cases except one on or immediately adjacent to a hackberry tree, confirming Austin's (1977) result. Some sites were occupied more frequently than others. In 97 censuses made over 17 days the average occupation frequency among the 20 perch sites was $21.9 \pm 20.6\%$; however, the two most frequently occupied sites were occupied in 83.5% and 61.9% of the censuses, respectively. Only one of the hackberry clumps in the study area never had a male perched next to it.

The behavior of the males followed a daily pattern. Males occupied perch sites when they first became active in the morning. Fig. 1 shows the number of males seen perching as a function of the time before and after the observed time of peak activity. Peak activity was defined as the time at which the number of sites occupied reached the maximum number observed on a given day. The average time of peak activity was 900 MST (range: 800-1000). Late in the morning the males moved into the shade of hackberry trees and became inactive.

Site Tenacity of Males

One-hundred and two males were captured, marked, and released. Of these 34% were resighted at some point after release (Fig. 2). After being marked and released, a male typically left the area and was not seen again on that day. The probability that a marked male would be resighted was highest the day after marking (18%). The longest time between release and the last resighting of a male was 10 days.

A male did not occupy a given perch site for long. Fig. 3 shows the distribution of site occupation durations observed on single days during the study. Most males were on a site for only 30 min or less on any given day. However, one male was observed on the most frequently occupied
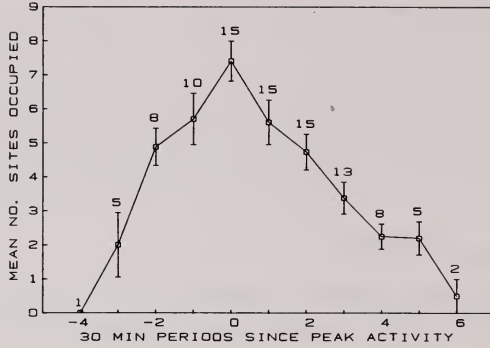
Fig. 1. The daily pattern of perching activity for *A. leilia* males averaged over 17 days. The number above each indicates the sample size.
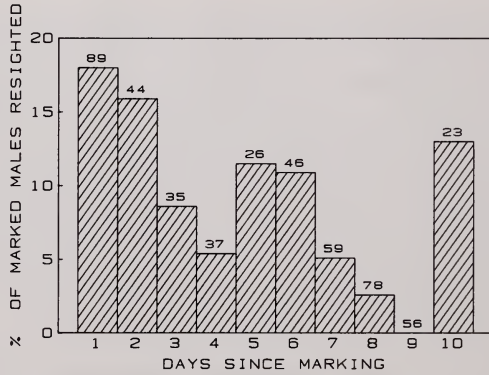

Fig. 2. The probability of resighting previously marked males as a function of the days since they were marked. The number above each bar is the number of males in the population marked on day zero that were available on a given day for recapture.
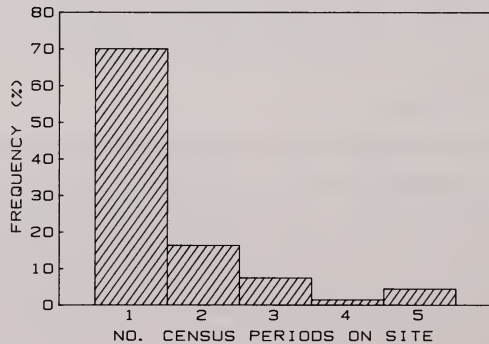

Fig. 3. For all sites that were seen occupied by a marked male this figure shows the duration of site occupation as the number of consecutive census periods on the same day that the male was seen on a given site (n = 67).

site on the study area for 5 census periods one day and then two more on the next. It is possible our censusing activities scared males prematurely from their perch sites; some males did take to wing when we approached but they returned to their perch after a brief flight. In any event we took some pains not to disturb males during the censuses.

Site Defense

Males perched on sand, rocks, and low vegetation (especially the hackberry tree) (Fig. 4). From these positions a male flew out and chased passing conspecifics, heterospecific butterflies, other insects (flies, wasps, etc.), birds, and even thrown stones. Conspecific males flying near a male's perch were typically approached and chased on the wing for several meters. In this species, no male-male interactions led to ascending flights. Occasionally a male perched near the resident without being detected. Such intruders were not detected until they flew, at which point they were approached and chased from the area. In 73% of 37 male-male interactions involving at least one marked male, the male that was originally perched in the area returned alone and reoccupied the site. This is significantly more frequently than expected from chance ($\chi^2 = 7.81$, 1 df, $p < 0.05$).

On occasion a male spontaneously flew up from his perch and patrolled an area by flying back and forth in front of the hackberry tree for a few seconds before perching again. When the resident alit after such a patrol flight or after an interaction he typically perched on or within a meter of his original perch.

The behavior of the males varied with the site and with the time of the morning. The more attractive sites were more likely to be occupied for more than one period by a single male (Table 1; $\chi^2 = 11.5$, 1 dr, $p < 0.05$). Males that occupied the two most popular sites tended to stay on them throughout the activity period in spite of frequent intrusions by other males. Eighteen perched intruders were observed at these sites in 528 min of observations during the hour surrounding the time of peak

Table 1. How site identity affects the number of consecutive census periods that the site will be occupied by the same male. Sites 1N and 15 were the most frequently occupied sites.

No. of periods occupied	Sites 1N and 15	All other sites
1	39%	82%
2-3	39%	18%
4-5	22%	0%
Total observations	18	49

Fig. 4.   Males of *A. leilia* perched on their sites. A male perched on staghorn cholla (above) and on the ground (below).

activity, while no perched intruders were observed in 107 min of observations on other sites at the same time.

Males do spontaneously abandon sites. Some sites were less likely to be abandoned for no apparent reason than less attractive sites. For example, during a total of 803 min of observation at sites 15 and 1N only one abandonment was observed. In contrast 6 abandonments were observed in 111 minutes of observations at three other sites (1S, 3S, and 3N) during the same time period. There were significantly fewer abandonments at site 15 and 1N than expected from the time spent observing there $\chi^2 = 35.5$, 1 df, p < 0.05).

Competition for sites is intense as indicated by the fact that when we sequentially removed 10 males during one hour from the most frequently occupied site, the site was reoccupied within a few minutes by a new male after each removal. Furthermore, the intensity of the competition changed over the morning. This was evident in two ways. First, if a male observed on a site in one census was not there when the site was censused 30 min later, at the time of peak activity there was a greater than 50% chance that the site would be occupied by a new male (Fig. 5). Late in the morning sites were rarely reoccupied if for some reason the male left. Second, the frequency of perched intruders waned as the morning progressed (Fig. 6; Spearman rank correlation coefficient = −0.87, p < 0.05).

Courtship and Copulation

The rate of appearance of wild females varied among sites. Females appeared at a rate of 0.0177 per min (790 min of observation) and 0.0123 per min at (163 min of observation) at the first and second most frequently occupied sites, respectively. In contrast, during a total of 203 min of observation no females were seen at several other sites when a male was present.

A total of 6 successful and 8 unsuccessful courtships were observed during this study. All successful courtships involved hand-reared virgin females released near males. On three occasions during observations of males on sites the male chased a female and did not return; the pair flew off so quickly we were unable to determine the outcome of the interaction.

When a female flew by a perched male he immediately took wing and followed the female. In successful courtships the female immediately perched in vegetation near the male's perch site. The male then landed behind the female, moved up beside her, and began attempting to insert his abdomen between the female's hindwings. The female then either remained still and permitted the male to couple or moved away from the male for some time before becoming still and permitting copulation. In unsuccessful courtship the female did not perch when the male approached and in 5 cases engaged in ascending flights with the male in pursuit. The male abandoned the female and returned to his perch after an ascending flight interaction.
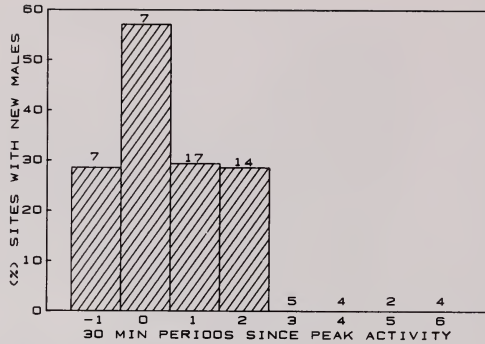
Fig. 5.   The likelihood that a previously occupied site will be occupied by a new
male in the census period after the site was seen to be occupied is plotted
against the time of the post-occupation census. The sample size for each
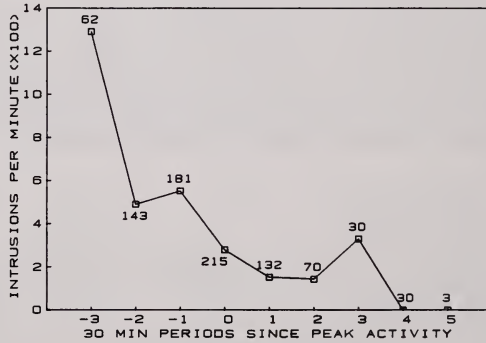time period is shown above each bar.

Fig. 6.   The rate of appearance of undetected perched intruders is shown as a
function of the time since peak activity. The number of minutes of
observation from which the data point was calculated is shown above each
point.

Copulation averaged 49 ± 16.8 min (n = 6, range: $21 - 65$ min).
During copulation a male formed a spermatophore and deposited some
loose white secretions within the female's bursa copulatrix. The mass of
material averaged 2.49 ± 0.78 mg (n = 7, range: $1.47 - 3.73$ mg) which
correspond to $2.96\% \pm 0.59\%$ (n = 7, range: $1.9 - 3.71\%$) of the male's
estimated precopulatory body weight. The quantity of material passed
was significantly positively correlated with the estimate of a male's
precopulatory body weight ($r = 0.797$, $t = 2.96$, 5 df, $p < 0.05$).

Twenty-six females were collected in the field and the contents of the
bursa copulatrix of each was examined. In this sample 73% were fresh,
19% worn, and 7% very worn. No female carried more than one
spermatophore and three (all fresh) had bursae that were empty.

DISCUSSION
Characteristics of Male Perching Behavior

The data reveal several features of the perching behavior of *A. leilia*. First, as Austin (1977) suggested, males perch most often near *C. pallida* trees. Second, a perched male does not tolerate other males in their perching area but are not likely to defend any given perch site for long. Third, males occupy and defend perch sites for only a restricted part of the day. Males became inactive toward the middle of the day and roosted well within *C. pallida* trees on or near their site. Such temporal restrictions on site-tenacious strategies of mate-location are common in butterflies (Callaghan, 1982; Alcock, 1983; Wickman, 1985) and are probably best explained by heat stress due to high midday temperatures (Rawlins, 1980; Kingsolver and Watt, 1983) which favors abandonment of perches in the late morning or by variation during the day in the availability of receptive females. Fourth, some sites are strongly pre- ferred over others as indicated by the frequency with which they were occupied, the rate at which undetected intruders perched on them, and the rate with which they were abandoned by males. Similar preferences are found in other perching species (e.g. Bitzer & Shaw, 1979; Leder- house, 1982; Alcock, 1983). Finally, the sites that were preferred by males were also those visited most frequently by females although it is not clear that these females were receptive. This has been shown for three other territorial species of butterflies (Davies, 1978; Lederhouse, 1982; Wickman, 1985).

The Function of Male Perch Site Placement and Defense

We interpret site occupation and defense as a mate-locating tactic in this butterfly. The sites contained no nectar or water resources that might be of interest to males or females and so defense of resources for personal use or to gain access to females seems improbable. Why then are the sites on or next to the larval foodplant? There are at least two possible hypotheses. A male may perch near the larval foodplant to gain access to females that come to oviposit. Such behavior has been observed in bees, dungflies, odonates, and many other insects (Thornhill & Alcock, 1983). However, there are apparently no benefits from trying to intercept mated females in that *A. leilia* females mate only once.

We conclude that males perch near the larval foodplant to maximize their chances of contacting virgin females as they emerge on their first flight. However, this assumes that the larvae pupate on the larval foodplant. This is likely. We have found cast pupal skins on *C. pallida*, and the pupae bear a striking resemblance to the leaves of the host plant, suggesting that the larvae routinely pupate on the larval food- plant.

Why do males perch at some trees and not others? Females may prefer

certain trees as oviposition sites and therefore these trees are more likely to produce virgin females than others. We do not at this point know if females are more likely to oviposit on the trees preferred by males; we only know that females are more likely to appear there. It may also be that some trees provide better vantage points for looking for newly-emerged butterflies. We are currently testing this hypothesis by setting up large visual barriers and seeing if they affect male perch site selection.

Variation in Site Tenacity and Defense

Asterocampa leilia males fall somewhere in the middle of the spectrum of site tenacity and defense shown by male butterflies. Site tenacity and defense are typically closely tied. Some butterflies show essentially no site tenacity, such as the alfalfa butterfly (*Colias eurytheme* Boisduval). On the other hand, males of some species perch on and defend the same site during the activity period for several days (Davies, 1978; Suzuki, 1978; Lederhouse, 1982; Alcock, 1983, 1985; Knapton, 1985; Alcock & O'Neill, 1986). In *A. leilia* even the most attractive sites were occupied and defended for only a few consecutive 30 min census periods and rarely for more than one day. What ecological factors have favored this sort of behavior?

Site occupation and defense in butterflies is associated with mate location. Hence, the form of this behavior will depend on a complex interaction between the spatial and temporal distribution of receptive females and the density of competitors (Rutowski, 1984; Courtney & Parker, 1985; Odendaal et al., 1985; Alcock & O'Neill, 1986). Currently our understanding of this interaction awaits further detailed studies of mate-location in species that perch.

Spermatophore Size and Mating System Structure

Male butterflies expend energy in reproduction in two ways. The first is in mate location. The second is in making spermatophores which contain not only sperm but also accessory gland secretions that may be used by the female as nutrients for egg production (Rutowski, 1984). In species that engage in site defense we expect that the amount of effort put into site defense will be a major determinant of reproductive success. Although males that patrol also expend energy in mate location the cost of this can be ameliorrated by their ability to feed while searching for females. Vigilance during site defense precludes feeding and defended sites rarely contain nectar resources.

We predict, therefore, that in species in which males defend perch sites, the males will expend more on mate location and less on spermatophore production than in species in which the males patrol in search of mates. As expected, males of *A. leilia* (this study) and males of *Pararge aegeria* Linnaeus (Svard, 1985), another site defending species

(Davies, 1978; Wickman & Wiklund, 1983), produce spermatophores that are small in relation to their body weight (2-3%) compared with other species that have been examined. Rutowski et al. (1983) surveyed 10 species of butterflies in which males patrol in search of females and found that typically 6 to 7 percent of the male body weight was donated in each spermatophore. Further studies are needed to test the prediction that mating system structure is linked with the investment males make in nutrient contributions to their mates.

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